SEASONAL PATTERN IN THE TERRITORIAL DYNAMICS OF THE ARBOREAL ANT *OECOPHYLLA SMARAGDINA* (HYMENOPTERA: FORMICIDAE)[1]

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A 30-month field study on territorial dynamics of *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae) colonies in Varanasi, India, revealed a regular seasonal pattern in territorial organisation. Each colony exhibited a circannual rhythm pertaining to the size of the central territory (nesting trees) and the secondary territory (ground area). Incorporation of new nesting trees in the central territory showed a major peak in September and a smaller peak during March-April. In each colony, only one tree, located near the centre of the territory, was used continuously for a maximum duration (28 and 30 months in colony I and II respectively). In both the colonies, trees located at a distant from the centre of the colony territory were found to be incorporated in the central territory, during March-April and/or September each year. Ground area used by each colony was largest during September. The circannual rhythm of territorial organization may be related to the brood development and food requirements of the *Oecophylla smaragdina* colony. Thus, territorial expansion during September, each year, may be a fine-tuned evolutionary adaptation of the growing colony to the availability of insect prey during the southwest monsoon rains.

Key words: Arboreal ant, *Oecophylla smaragdina*, territorial dynamics, circannual rhythm, polydomous nest organization

INTRODUCTION

Territorial behaviour is shown by a number of ant species (Hölldobler and Wilson 1990). Territorial ant species with polydomous nest organization (several nests belonging to the same colony) are able to patrol and exploit large areas of their territory simultaneously, without incurring the costs of transporting prey from distant points of capture to a single central nest (e.g. in *Camponotous gigas*, Pfeiffer and Linsenmair 2000). A seasonal, spatio-temporal variation in the location and density of nests has been reported in the polydomous ant species *Myrmicaria opaciventris* colonies (Kenne and Déjean 1999). However, so far, no investigation has focused on the annual, seasonal pattern in the territory size of a polydomous, tropical ant species maintaining absolute, three-dimensional territories.

The arboreal ant *Oecophylla smaragdina* (Fabricius) makes a silk-lined nest of living leaves (Hingston 1927), and is strongly territorial (Hölldobler 1983). The worker ants patrol three-dimensional territories comprising the central territory consisting of the tree(s) used for nesting and the secondary territory, the ground (Déjean 1990). Colonies of *O. smaragdina* (from Asia and Australia) and its closely related species *O. longinoda* (from Africa) have polydomous nest organization, with a large number of leaf nests scattered over canopies of several trees, within the territory. Individual colonies may cover an area of up to 1,600 sq. m and comprise of about a million workers and brood (Way 1954; Hölldobler 1979). Information regarding the territorial dynamics of *O. smaragdina* colonies is of particular ecological interest and of economic significance, as *O. smaragdina* is the earliest known example of a biological control agent (Huang and Yang 1987) and is still used in China against citrus pests (Yang 1982). Both species of *Oecophylla* have been found to significantly reduce the number of a variety of insect pests of tropical crops, including Coconut *Cocos nucifera* (Vanderplank 1960), Cocoa *Theobroma cacao* (Room 1975) Mango *Mangifera indica* (Way 1954) and Coffee *Coffea arabica* (Leela 1961). In the present investigation, the territorial dynamics of *O. smaragdina* colonies have been studied for two and a half years, to examine the seasonal, annual pattern in the size of the central and secondary territories.

STUDY AREA AND METHODOLOGY

This is part of a long-term field study carried out from July 1997 to December 1999 in the grounds of Banaras Hindu University Campus in Varanasi over an area of about 3,000 sq. m. The trees/shrubs occupied by *O. smaragdina* included *Mangifera indica* (Anacardiaceae), *Spondias pinnata* (Anacardiaceae); *Terminalia bellerica* (Combretaceae), *T. arjuna* (Combretaceae); *Psidium jambolana*, *P. guajava* (Myrtaceae); *Emblica officinalis* (Euphorbiaceae); *Mimusops elengi*, *Madhuka indica* (Saptoceae); *Erwatamia* sp., *Nerium indicum* (Apocynaceae); and *Hibiscus rosa-sinensis* (Malvaceae). The trees being about 25 years old were tall (*c.* 12-15 m) with dense canopy. Many of the nests were high up in the upper part of the canopy while others were in the peripheral parts of the canopy. While some of the peripheral nests were clearly seen, it was

difficult to detect and count all the nests of *O. smaragdina* on each tree.

In the study area, *O. smaragdina* colonies were demarcated by experimental, forcible confrontation of marked workers (by using quick drying paints) to conspecifics present at the base of other tree trunks (Hölldobler 1983). The resident ants, on discovering intruders belonging to alien colonies, lunged at them, bit and pulled their appendages singly or in groups till all the intruders were killed. Thereafter, the residents moved up the tree trunks carrying the killed intruder ants, to their nests. Introduction of marked workers at the base of the parent tree trunk/on the ground area used by ants of the same colony, elicited simple antennation by the residents after which the introduced ant mingled with the residents and went up the tree trunks. The confrontation experiments were repeated five times, between conspecifics nesting on two different trees each time, using ten marked ants each, with five as control and five as experimental. Similarly, the foraging areas used by ants belonging to different colonies were demarcated. In this way, five colonies of *Oecophylla smaragdina* were distinguished in the field. However, two colonies were displaced by two different ant species; *Tetraponera allaborans* Walker and *Paratrechina longicornis* (Latr.) in August-September 1998, while the third colony, after three nest relocations in 1997 and one in 1998, could not be traced further in the field. Therefore, the seasonal changes in the territory size could be recorded continuously for 30 months only for territories of two colonies designated as colony I and II.

The number of trees/shrubs used by *O. smaragdina* workers for nesting and/or descending to the ground level for foraging/patrolling was recorded four times each month except during June each year. The presence/absence of nests was also recorded on the trees/shrubs during these observations, each month.

The ground area was marked into grids (each quadrant = I sq. m). Each quadrant was scanned (this involved walking the ground and taking observations for *c.* 3-4 hours per day, twice a week, during the study period; total *c.* 768 hours during 36 months) for the presence/absence of the foragers during the peak morning foraging hours (from 0800 to 1200 hrs). The data was recorded on a grid map four times a month for each colony from July 1997 to November 1999, except during June, December, January and February (the peak summer and winter seasons) when foraging activity was found to be reduced. The worker ants showed no foraging activity on cloudy days with maximum day temperature of 19° C during winter season. Observation of the leaf nests indicated that the foragers did not leave the nests. Data is given as mean ± S.E.M. Results were statistically analysed using Student's *t* test.

The centre of the ground area patrolled by workers of each colony was determined by finding the values of the X and Y co-ordinates at 164 different points along the boundary of the territory of colony I and at 150 different points along the boundary of the territory of colony II.

RESULTS

Seasonal variation in the number of nesting trees used (central territory): The number of nesting trees/shrubs used by a colony at a time varied from 2 to 8 (4.83 ±0.0163) for colony I and 1 to 7 (2.76 ±0.011) for colony II. The number of trees used by workers of each colony to descend to the ground to forage showed one small peak in March-April and a main

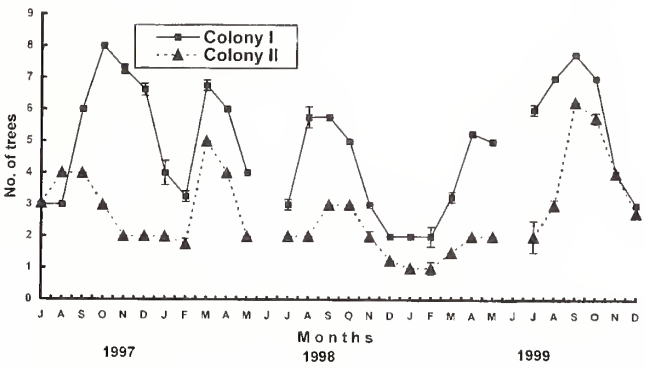

Fig. 1: Number of trees used (Mean ± S.E.M.) for nesting and/or descending to ground level by workers of *O. smaragdina* colony I and colony II during various months from July 1997-December 1999

peak in September/September-October each year (Fig. 1). The number of nesting trees used during April differed significantly as compared to January, February and May (df =14, $p<0.001$ for colony I and $p<0.005$ for colony II for each month), but was not significantly different with respect to March. (df=14, $p>0.5$). The number of nesting trees used during September was significantly higher with respect to July, August, November and December (df=22, $p<0.001$ and $p<0.05$, $p<0.005$ and $p<0.01$ for colony I and df = 99, $p<0.001$, $p<0.05$, $p<0.005$, $p<0.001$ for colony II respectively). It did not differ significantly with respect to October (df =22, $p>0.5$). With the onset of summer (May) and winter (December-February) number of trees used by each colony decreased sharply each year (Fig. 1). Seventeen trees and nine shrubs were used in total, at various times by colony I and II foragers respectively.

Duration of use for each tree: Duration for which each tree was used for nesting varied from 1 to 28 (5.92 ±1.32) months and 1 to 30 (9.15 ±2.14) months for colony I and colony II, respectively (Figs 2a, 2b). Tree 'G' and tree 'c' were found to be used continuously for a maximum duration of 28 and 30

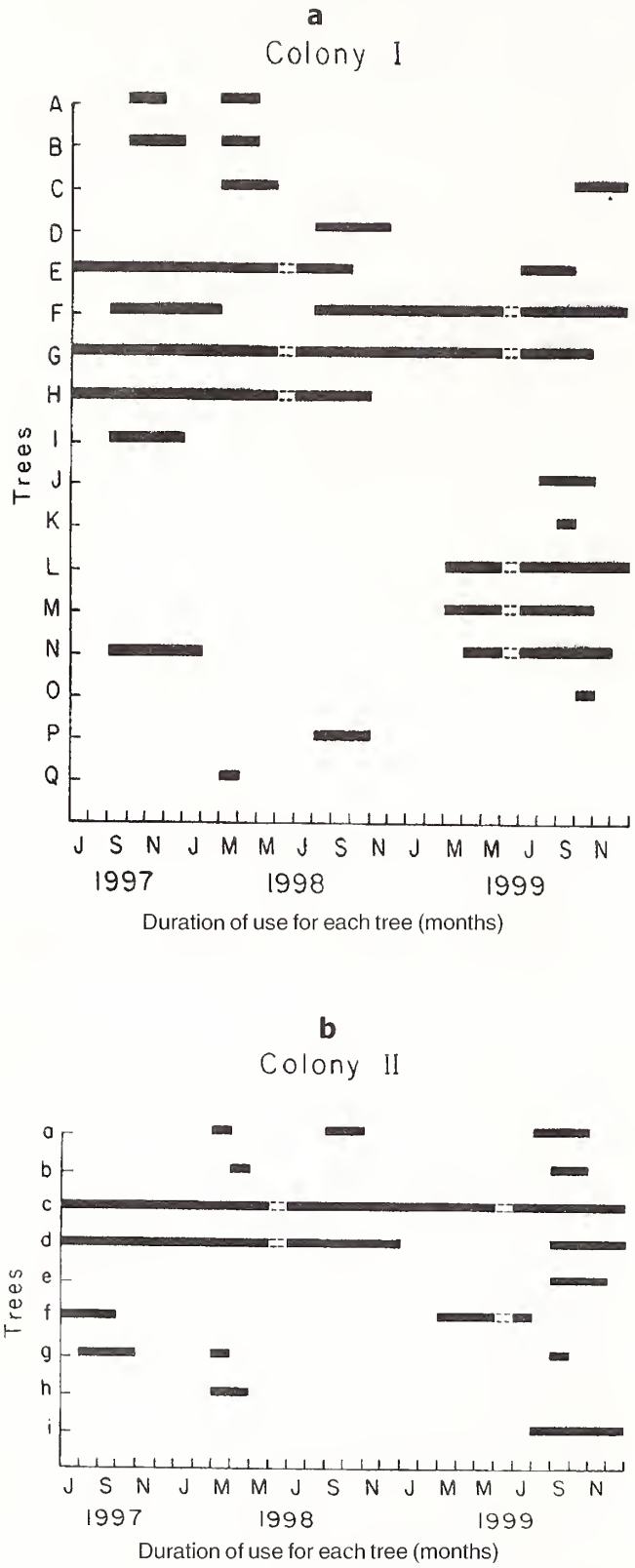

Fig. 2 a & b: Time duration of use (in months) of the trees/shrubs used for nesting/ descending to the ground for foraging in each colony (a) colony I (b) colony II, from July 1997 to December 1999

months in colony I and II, respectively and were found to occupy an approximate central location in the territory patrolled by the colony (Figs 3a, 3b). The canopy of tree 'G' was found to be in contact with those of trees/shrubs B, C, D, E, F, H, I, J, N, and P, either directly or indirectly. In colony II, canopy of tree 'c' was found to be in direct or indirect contact with the canopies of trees/shrubs of a, b, d, e, f, g and h.

In colony I, trees E, F, G, H, L, M, N were used for long periods (5-28 months, 11.4 ±0.792) and in colony II, trees 'c' and 'd' were used for long periods (4-30 months, 17.33 ±5.31). They were found to have some common features, tall and dense canopy, location close to the centre of the ground territory and direct canopy contact with tree 'G'/ 'c'. Trees with small, sparse canopy (J, K) or distantly located from the centre, and/or in indirect (or without) canopy contact with tree 'G' (trees A, B, C, D, O, P, and Q in colony I) or tree 'c' (trees a, b, e, f, g, h and i in colony II) were incorporated in the central territory only in March-April and/or September.

Seasonal variation in the ground (secondary) territory used: Ground territory patrolled and defended at a particular time by workers of colony I varied from 61 to 540 sq. m (217 ±0.92), and that of colony II ranged from 38 to 295 sq. m (106.45 ±0.68). The ground area defended by an *O. smaragdina* colony was found to increase rapidly from July to September each year, in each of the colonies (Figs 4a, 4b). In both, the ground area patrolled during September was significantly larger with respect to March, April and May ($df=18$, $p<0.005$, $p<0.001$, $p<0.005$ in colony I and $p<0.001$, $p<0.005$, $p<0.001$ in colony II, respectively). It was also significantly larger as compared to July, August, October and November ($df=22$, $p<0.001$, $p<0.05$, $p<0.001$ in colony I and $p<0.001$, $p<0.005$, $p<0.05$, $p<0.001$ in colony II, respectively).

DISCUSSION

The present study clearly shows that the central and secondary territory used by each *O. smaragdina* colony show an annual, seasonal variation in size. Recently, Wuellner and Saunders (2003) found circannual patterns of activity in *Solenopsis geminata* (F.) and *S. invicta* Buren workers. While the former showed no activity, the latter showed reduced activity above the ground during the coldest months, November through February.

This long-term investigation reveals that *O. smaragdina* exhibits a circannual rhythm in the number of trees (central territory) used by the foragers of a colony to descend to the ground level and in the size of the ground area (secondary territory), patrolled and foraged. Incorporation of new nesting trees showed a small peak during March-April and main peak during September each year, in each colony. On the other

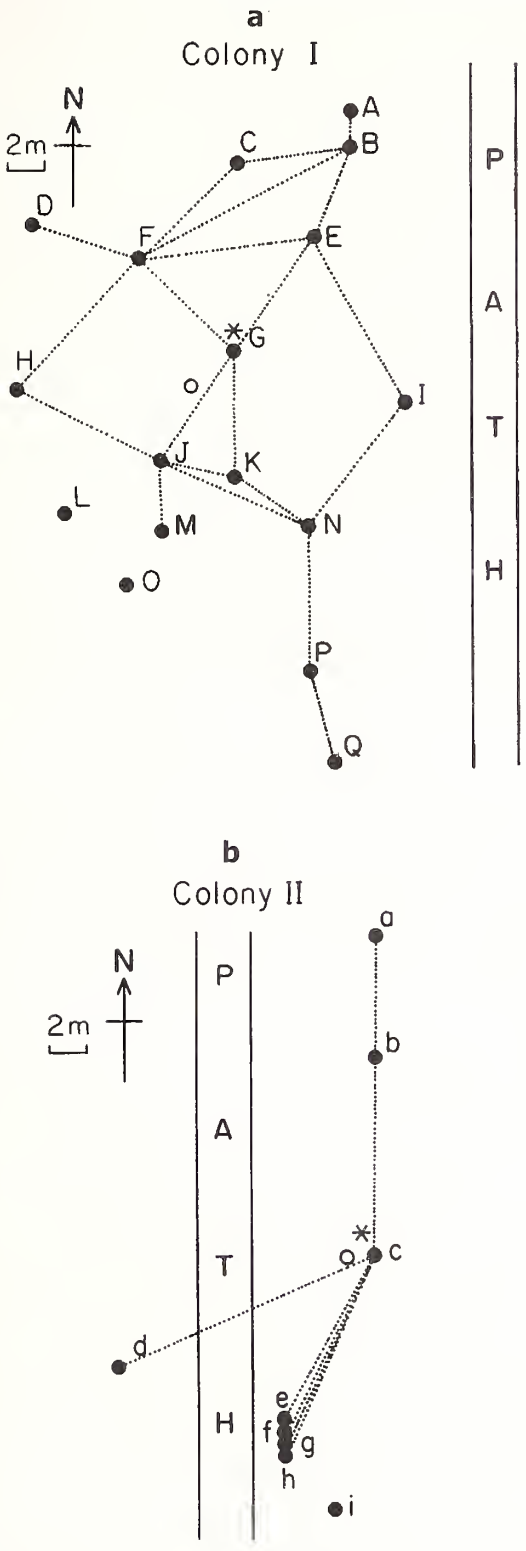

Fig. 3 a & b: Canopy contacts between trees/shrubs used for nesting by (a) ants of colony I and (b) ants of colony II. Asterisks denote the tree 'G' with central location used for maximum duration of 28 months in colony I and tree 'c' with central location in colony II and used for maximum duration of 30 months. Open circle denotes the center of each territory and closed circles denote the location of nesting trees/shrubs in territory of each colony

hand, the largest ground area was patrolled only during September each year. I suggest that the increase in the size of the ground territory, beginning in July and reaching a peak value in September, is probably correlated to the increase in the food requirements of the colony, which may be an adaptation to the availability of insect prey during the rainy season. In the northern plains of India, including Varanasi, the southwest monsoon retreats by the end-September so that rainfall ceases by October (Srivastava 2001). During October, the territory size decreases rapidly (Figs 4a, 4b). Thus, rainfall (along with temperature conditions) may be an important abiotic factor influencing territory size, though the basic territory size regulating factor is suggested to be the food requirements of the developing colony. On the basis of the present data it is difficult to explain the gradual decline in

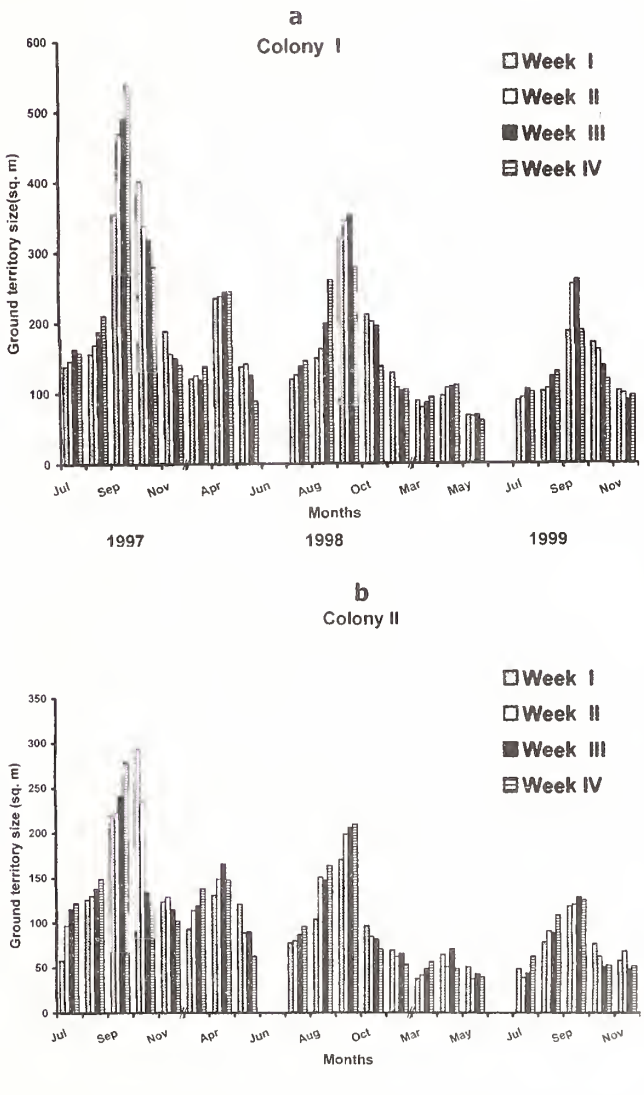

Fig. 4 a & b: Ground territory size of *O. smaragdina* (a) colony I and (b) colony II during each week, in different months, during three years: July-November 1997, from March-November 1998 & 1999

the peak value for the ground territory patrolled, from 1997 to 1999 in both colonies.

Seasonal variation in nest density, with density being higher during the rainy season, as compared to the dry season, and characterized by the disappearance of many nests at the end of the main rainy season, has also been reported in the polydomous colonies of *Myrmicaria opaciventris* Emery (Kenne and Déjean 1999). They have also recorded the exploitation of vast distant areas by means of underground tunnels in this polydomous ant species. Thus, polydomous nest organization, whether on the ground or on the tree canopy, facilitates efficient foraging over large areas during the favourable season. I suggest that *O. smaragdina* colonies initiate expansion of the central territories by using new trees in spring to meet the space requirements of the developing colony. Territorial expansion of the central and ground territories in autumn is suggested to be related to the increased food and space requirements of the developing brood. The circannual rhythm of territorial expansion in *O. smaragdina* is suggested to be correlated to the reproductive phase of the colony, since brood development may be serving as the proximate cue for increase in the number of nesting trees used (central territory) and expansion of the secondary territory on the ground. The correlation of the timing of nest building with the abundance of immature offspring and the coincidence of building with the start of the period when food availability reaches its peak in the habitat has been demonstrated by Fernandez-Escudero *et al.* (2001) in the polygynous, polydomous ant species *Proformica longiseta*. A circannual rhythm in the territory size probably enables the populous *O. smaragdina* colonies to be prepared for favourable conditions (during the rainy season) when food (prey) is abundant.

Tree 'G' in colony I and 'c' in colony II with maximum duration of uninterrupted use and approximate central location in the colony territory, may be harbouring the queen nest. Although further work is needed to confirm that the queen nest is in the central tree; since workers carry the eggs to other nests in the colony, central location of queen occupied trees may be playing an important role in facilitating worker movements to the nests on the canopies of other trees. Thus, trees distantly located from tree 'G' and 'c' are used only at the time of favourable conditions and maximum territory use.

The information presented here, on the seasonal pattern in the territorial dynamics of *O. smaragdina*, is of significance as it can be used in context of the use of *O. smaragdina* as a biocontrol agent (DeBach and Rosen 1991; Hill 1983).

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